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Reproductive biology of *Spondias tuberosa* Arruda (Anacardiaceae), an endemic fructiferous species of the caatinga (dry forest), under different management conditions in northeastern Brazil

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ABSTRACT

In areas under different management conditions (management units, MUs) located either on a slope or at the base of a slope and either in a plantation or in a pasture, we compared the flower and fruit production, floral visitors, visitation rates and pre-emergent reproductive success (PERS) of *Spondias tuberosa* (Anacardiaceae) in an area of dry forest in NE Brazil. Individuals in the plantation MU produced more flowers per inflorescence than those in other MUs, but there were no statistical differences in mean fruit set among MUs. The only difference in mean visitation rates was between the plantation (65.83 ± 38.49) and the slope sites (11.5 ± 12.8). We observed visits by 19 insect species, including bees (31.6%), butterflies (31.6%), wasps (26.3%) and flies (10.5%). A clustering analysis based on the number of visits showed that a) the plantation site is most different from the other MUs, b) the pasture and the site at the base of the slope are similar to the slope site, and c) the higher frequency of visits of pollinators in the plantation MU was responsible for these differences. Of the 19 species of insects visiting the flowers, 12 were considered pollinators. The pollinator similarity analysis indicated a clear separation between areas and suggested that human activity has resulted in the replacement of native pollinators by exotic species. However, these changes apparently have not affected the pre-emergent reproductive success of *S. tuberosa*. Our results show that plant reproductive biology in semi-arid ecosystems may be modified by human action and that changes in floral production and pollinator guilds are the most conspicuous effects. However, the traditional management performed by local people may not affect the reproductive success of plant species.

1. Introduction

Humankind has caused many alterations to natural habitats (Albuquerque, 1999; Casas et al., 1999; Pesci, 2004). Most anthropogenic pressure on natural habitats is related to agriculture and pasture establishment, for which various management strategies are used (Sampaio, 2002). Management strategies vary from totally destructive (and unfortunately broadly applied) methods, such as complete deforestation (Salick, 1995), to management of native vegetation (Moonen and Barberi, 2008). Deforestation causes habitat fragmentation (Saunders et al., 1991; Aizen and Feinzinger, 1994a,b; Fischer and Lindenmayer, 2007), which is considered to be one of the most severe threats to biodiversity conservation (Fischer and Lindenmayer, 2007). Habitat fragmentation may result in important changes in both abiotic and biotic conditions (Saunders et al., 1991; Cunningham, 2001) and in the alteration and/or interruption of ecological processes, such as those related to plant reproduction (Tabarelli et al., 2004; Lopes et al., 2009). The isolation of individuals in the landscape constitutes a barrier to effective pollination and seed dispersal (Aizen and Feinzinger, 1994a; Silva and Tabarelli, 2000), affecting gene flow and population genetics (Couvet, 2001).

Plant reproductive features, such as pollination and sexual and breeding systems, have been used to understand plant responses to environmental changes. Most studies indicate that habitat transformation has negative consequences for reproductive success in both humid (Ghazoul and McLeish, 2001; Murren, 2002) and arid (Aizen and Feinzinger, 1994a; Fuchs et al., 2003; Quesada et al., 2004) ecosystems. On the other hand, some species apparently present positive changes in their reproductive strategies after habitat alteration, such as enhanced flower production in both

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types of environments (Murren, 2002; Fuchs et al., 2003; Quesada et al., 2004).

Although many studies have pointed out the negative impact of anthropogenic actions upon biodiversity, only a few studies have evaluated specific components of this impact, such as species selection criteria, historic land use and patterns of land occupation (Wyman et al., 2007). Closer study of these aspects will help us to understand the influence of habitat fragmentation upon ecological processes (Albuquerque, 1999; Araújo et al., 2007). Examples of this type of study include the work of Oaxaca-Villa et al. (2006), Arias-Cóyotl et al. (2006), Casas et al. (1999) and Lira and Casas (1998) concerning Cactaceae species that are used as a food source by people in a semi-arid region in central Mexico. Although these studies have revealed important aspects of changes in plant reproductive biology after habitat alteration, more studies that relate patterns of environment management to plant reproductive biology in arid and semi-arid ecosystems are clearly needed.

The caatinga is a dry forest ecosystem exclusive to Brazil that occupies an area of about 800,000 km^2; in the northeastern part of the country (Leal et al., 2003). The caatinga constitutes an excellent natural laboratory for studies of human–plant interactions (Araújo et al., 2007). For centuries, human activities have changed the environment of the caatinga. The most important human impacts are related to agriculture, cattle breeding and the extraction of woody products (Sampaio, 2002). These activities probably influence plant reproduction, as has been recorded in other semi-arid ecosystems of the world (Lira and Casas, 1998; Casas et al., 1999).

Spondias tuberosa (Anacardiaceae), locally called "umbuzeiro", is a tree species averaging about 6 m tall (Santos, 1997) that is endemic to the caatinga (Giulietti et al., 2002). It is andromonoecious and self-incompatible and has a generalist pollination system, pollinated mainly by bees and wasps (Machado and Lopes, 2004; Nadia et al., 2007; Barreto, 2007). *S. tuberosa* produces flowers and fruits during the dry season (Nadia et al., 2007), when most plant species remain in a completely deciduous state (Araújo et al., 2007). Thus, the species represents an important resource for pollinators and dispersers during the dry season. Moreover, the fruits represent an income supplement for the local people, as they are used as food for humans and cattle (Cavalcanti et al., 2000a; Lins Neto et al., 2010). Thus, the species has great importance in ecological, social, economic and cultural contexts (Barreto, 2007; Nadia et al., 2007; Lins Neto et al., 2010).

Researchers have studied several aspects of *S. tuberosa*, such as its genetics (Santos, 1997), physiology (Cavalcanti et al., 2001), conservation and trade (Cavalcanti et al., 2000a, b), ethnoentomology (Barreto, 2007) and reproductive biology (Leite, 2006; Barreto, 2007; Nadia et al., 2007). However, no data have been previously published on the influence of different types of management on the reproduction of *S. tuberosa*.

The objective of this study is to answer the following question: can human impacts (from an ethnobotanical point of view) on natural semi-arid environments affect the reproduction of *S. tuberosa*? More specifically, we investigate flower and fruit production, floral visitor guilds and the frequency of visits to flowers as functions of different management types in an area of caatinga vegetation in northeastern Brazil.

2. Material and methods

2.1. Study area

The study was performed in the rural community of Carão, located 16 km from the centre of Altinho municipality, Pernambuco state (08°29′23″S, 36°03′34″W), with an altitude of 450 m (CONDEPE/FIDEM, 2007). The climate is hot and semi-arid (BSh *sensu* Köppen) with an annual mean temperature of 23 °C, marked climatic seasonality, and caatinga vegetation (CONDEPE/FIDEM, 2007).

Significant transformations in plant cover have occurred in the region that is related to the type of land use (e.g., for pasture, permanent and/or temporary plantations and extraction of woody forest resources). Four functional units may be identified in the landscape, characterized by distinct types of soil and/or of vegetation cover. In this study, these units are referred to as management units (hereafter MUs). Individuals of *S. tuberosa* are found in all MUs (Fig. 1). In MUs with plantations or pastures, people do not cut individuals of this species, which remain isolated in the landscape. The identification of MUs is easy for both local people and scientists. The areas chosen for this study were selected following a community mapping activity conducted by Lins Neto et al. (2010). The MUs are described as follows:

Slope – The "Serra do Letreiro" region is a moderately sloping area (altitude of 690 m) adjacent to the Carão community that presents caatinga vegetation (Lins Neto et al., 2010). Shrubs and trees predominate, reaching 10 m in height and more than 50 cm in diameter at soil level. Important tree species include *Myracrodruon urundeuva* Fr. All. (Anacardiaceae), *Schinopsis brasiliensis* Engl. (Anacardiaceae) and *Anadenanthera colubrina* (Vell.) Brenan (Mimosaceae); important shrubs include *Caesalpinia pyramidalis* Tul. (Caesalpiniaceae) and *Croton blanchetianus* Baill. (Euphorbiaceae). Parts of this area were deforested 60 years ago and used for subsistence farming. However, local people informed us that farming activities ceased several decades ago on the steeper parts of the slope, where the caatinga vegetation has been regenerating for 30–50 years. These areas are frequently used for the extraction of forest resources, such as firewood, coal and medicinal plants (Araújo et al., 2008; Alencar et al., 2009,2010; Santos et al., 2009).

Base of slope – This is the transitional area between the slope and the prairie regions that are used for farming and pastures. The altitude varies from 460 to 520 m, and there are both level and sloping regions within this MU. In addition to altitude, the physiognomy and the apparently less-advanced degree of regeneration are the main differences between this MU and the slope MU; this regeneration has occurred within the last ten to fifteen years. The base-of-slope MU presents dry, shrubby vegetation about 3 m tall, with some trees. The most frequent species is *C. blanchetianus*. The vegetation of this MU is extracted for firewood (for domestic use) and for the construction of small buildings.

Pasture – Located in prairie areas with altitudes from 440 to 460 m, pasture areas present predominantly herbaceous vegetation where cows and goats livestock are pastured. Natural vegetation has been totally suppressed for about the past 30 years. People frequently cut shrub and tree individuals that germinate, with the exception of *S. tuberosa* and some Cactaceae species, which are used as a food supply for cattle during the dry period (Santos et al., 2009).

Plantation – Like pastures, plantations are located in the prairie, but they are more frequently used for the cultivation of corn, beans and *Opuntia ficus-indica* Mill (Cactaceae). Soil preparation occurs at the end of the dry season, when people cut and burn woody and herbaceous elements (except for *S. tuberosa* and Cactaceae species), and the soil is bare at the beginning of the wet season.

Within each MU, we labeled 15 individuals of *S. tuberosa*. Each individual was of similar size, had reached reproductive maturity, and had a distance of less than 3 m between the soil and the crown (to facilitate access to flowers). In addition, each individual was located at least 50 m from other labeled individuals to avoid sampling clones because this species presents vegetative reproduction (see Araújo and Oliveira, 2008).

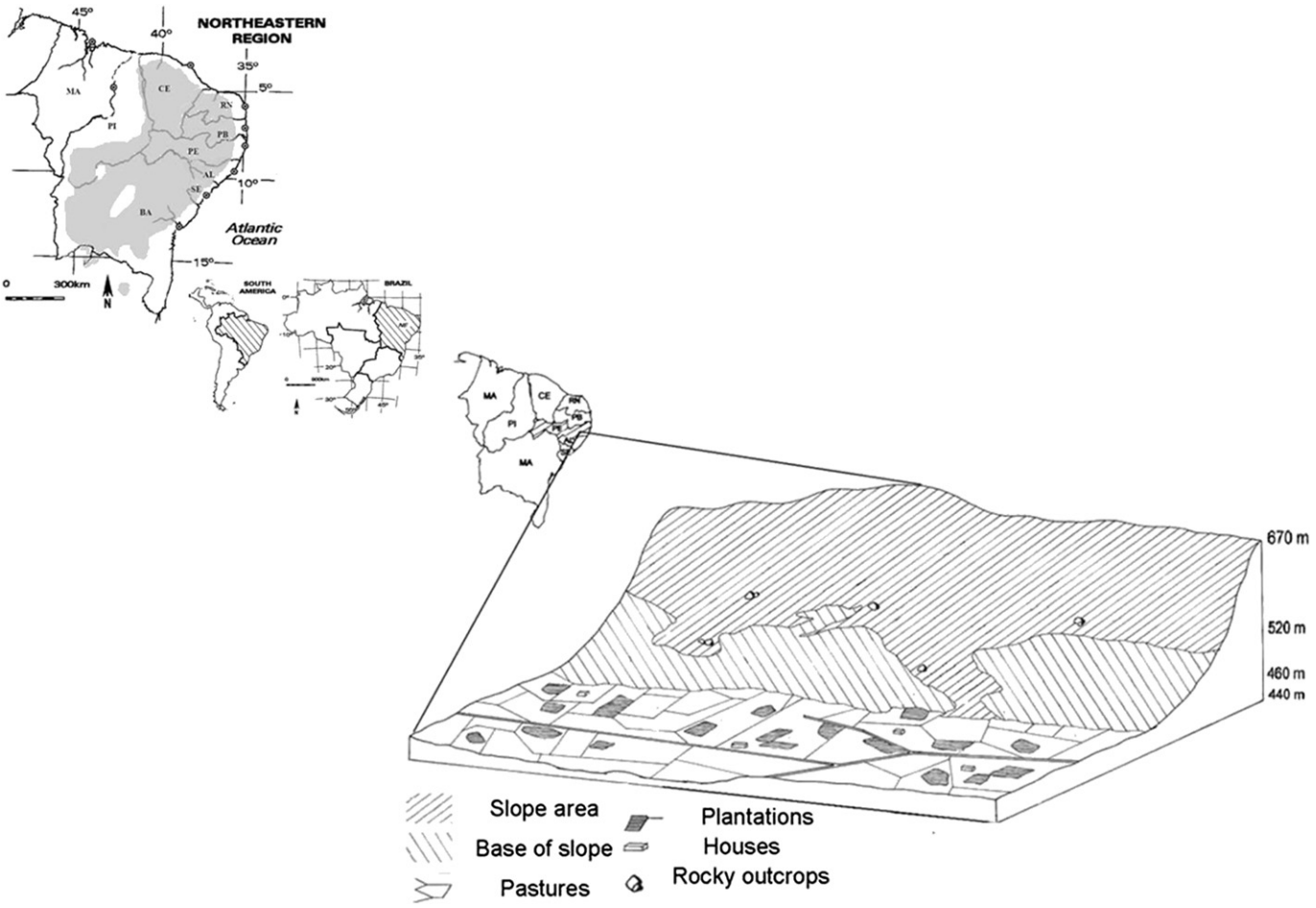

Fig. 1. Schematic topographic representation of the study area, showing the respective management units. Altitudinal scale is related to sea level. A: Map showing the location of the Caatinga domain (gray) from Araújo et al. (2007).

2.2. Data collection

2.2.1. Flower and fruit production

The mean number of flowers per inflorescence was estimated by counting buds and flowers from 15 inflorescences of each of the 60 selected individuals (900 inflorescences total).

The mean number of fruits per inflorescence was estimated by counting hermaphroditic flowers from five pre-anthesis inflorescences in all labeled individuals and recording fruit set after 15 days (300 inflorescences total; Barreto, 2007; Nadia et al., 2007). The number of hermaphroditic flowers per inflorescence was estimated using the mean number of hermaphroditic flowers obtained for each MU. The pre-emergent reproductive success (PERS) was calculated for each MU as the ratio between the number of fruits and the estimated number of hermaphroditic flowers per inflorescence. This formula, adapted from Wiens et al. (1987), also provided the seed/ovule ratio, which is 1:1 for *S. tuberosa* (Leite, 2006; Nadia et al., 2007).

2.2.2. Floral visitor guild

The frequency and behavior of floral visitors were observed between October 2007 and March 2008 (thus including all flowering periods; Nadia et al., 2007). All data were collected under similar weather and phenological conditions, following Nadia et al. (2007). The focal observations were made in the lower parts of the crown, in ten inflorescences of five individuals in each MU (200 inflorescences total). The observations occurred between 5:00 h and 17:00 h in sessions of 30 min in odd hours during one field trip and in even hours during the next trip. Thus, we performed observations during the morning and evening in each MU, for a total of 18 h of observation throughout the flowering period (72 h total).

During the pollinator visits, we recorded the provisional name of the floral visitor (to facilitate field work), the number of flowers visited and the pollinating behavior, such as contact with sexual structures, kind of reward used and interactions with other visitors. Depending on the frequency of visits and on behavior, floral visitors were classified as effective pollinators (those that contacted sexual structures and visited frequently), occasional pollinators (those that contacted sexual structures but visited infrequently) and robbers (those whose morphological and/or behavioral features prevented contact with sexual structures).

Floral visitors were collected, identified by specialists and deposited in the Laboratório de Biologia Reprodutiva de Angiospermas collection at the Universidade Federal Rural de Pernambuco.

2.3. Data analysis

The mean number of flowers per inflorescence was compared among the four MUs using the non-parametric Kruskal–Wallis test. Normality was verified using the Shapiro–Wilk test (Zar, 1996) with data transformed by a log *n* function. Differences between the

Table 1
Number of flowers per inflorescence, sum of hermaphrodite flowers and reproductive success of *Spondias tuberosa* Arruda (Anacardiaceae) populations subjected to different management regimes in an area of caatinga vegetation in Altinho, Pernambuco, Brazil. Values are shown as mean ± standard deviation. Fl/infl: mean number of flowers per inflorescence; ∑ herm. flowers: sum of hermaphroditic flowers; Mean fr/infl: mean number of fruits per inflorescence; Fr/fl: number of fruits per inflorescence.

	Fl/infl (n = 900 infl)	∑ herm. flowers (n = 15 infl)	Mean fr/infl (n = 15 infl)	Fr/fl (n = 15 infl)
Slope	151.5 ± 49.5 a	352.9 ± 67.4 a	2.7 ± 2.6 a	0.8 ± 0.7 a
Base of Slope	137.8 ± 34.3 a	294 ± 69.2 b	1.4 ± 1 a	0.5 ± 0.3 a
Pasture	135.3 ± 39.8 a	378.1 ± 120 a	1.9 ± 1.6 a	0.5 ± 0.4 a
Plantation	175.7 ± 39.5 b	350 ± 84.7 a	1.4 ± 1.3 a	0.4 ± 0.41 a

Different letters within columns indicate significant differences according to the Kruskal–Wallis test. First column: H = 9.68; GL = 1; P = 0.02; other columns: H = 7.73; GL = 3; P = 0.049).

MUs in the number of floral visitor species were tested using the chi-square test (Zar, 1996). We used the Kruskal–Wallis test (Zar, 1996) to test for significant differences in the mean number of visits per day and to verify whether the visitation rate of certain species varied as a function of MU. The significance threshold was considered to be a probability of 5%.

The similarity of floral visitors between the MUs was tested using a clustering analysis (UPGMA). We conducted this analysis using species presence-absence data (with the Jaccard coefficient) (Valentin, 2000). All analyses except the similarity analysis (which was performed using the MVSP program) were performed using the program BioEstat version 4.0 (Ayres et al., 2003).

The experimental design did not allow the replication of management units (MUs), because we did not find more areas under similar conditions in the region, and we recognized this limitation in our interpretations.

3. Results

3.1. Flower production

Mean flower production per inflorescence was higher in individuals from the plantation MU (175.7 ± 39.5, mean ± standard deviation, H = 9.68; G.L. = 1, P = 0.02) than from the other habitats (pasture = 135.3 ± 39.8, base of slope = 137.8 ± 34.3 and slope = 151.5 ± 49.5). The values for the other three MUs were statistically similar (Table 1).

3.2. Fruits

We observed no significant differences among the MUs in mean number of fruits per inflorescence (H = 2.47, P = 0.47; Table 1). In all MUs, the fruit/flower ratio was very low: more than 50% of inflorescences did not set fruits, and most inflorescences that did set fruits produced only one (at least at the beginning of development). The development of two fruits was observed in only 8% and 4% of inflorescences in the slope and pasture MUs, respectively, and none of the inflorescences in the base-of-slope and plantation MUs developed two fruits. We found no significant differences among the MUs in PERS (H = 3.29; P = 0.34); the smallest value was recorded in the plantation MU (0.4%) and the largest value was recorded in the slope MU (0.77%).

3.3. Floral visitor and pollinator guilds

We recorded 772 visits to flowers of *S. tuberosa*, distributed as follows: 51.3% in the plantation MU, 21.7% in the pasture MU, 18% in the base-of-slope MU and 9% in the slope MU. The only significant difference in mean number of visits per field tree in each MU was between the plantation (65.8 ± 38.5) and the slope (11.5 ± 12.8; H = 7.41, P = 0.006) MUs.

Table 2
Floral visitors observed in populations of *Spondias tuberosa* Arruda (Anacardiaceae) subjected to different management regimes in an area of caatinga vegetation in Altinho, Pernambuco, Brazil (MU = management unit; S = slope, B = base of slope, Pa = pasture, Pl = plantation; p = pollen, n = nectar; P = pollinator, OP = occasional pollinator, R = robber).

Visitors	MU	Resource collected	Visitor type
HYMENOPTERA			
Apidae			
1- *Apis mellifera* L. 1758	S,B,Pa,Pl	p, n	P
2- *Centris* (Trachina) fuscata Lepeletier, 1841	Pa,Pl	p, n	P
3- *Frieseomelita* sp.	Pa	p, n	P
4- *Plebeia* sp.	B	n	R
5- *Trigona* sp.	S,B,Pa,Pl	p, n	P
6- Apidae 1	S,B,Pa,Pl	n	OP
Vespidae			
7- *Brachygastra lecheguana* (Latreille, 1824)	Pa,Pl	n	P
8- *Polistes canadensis* (L.1758)	S,B,Pa,Pl	n	P
9-*Polybia ignobilis*(Halliday, 1836)	S,B,Pa	n	P
10- *Polybia platycephala* Richards, 1978	B,Pa,Pl	n	P
11- *Zethus mexicanus* (L.)	S,B,Pa,Pl	n	P
DIPTERA			
12- Sarcophagidae	S,B,Pa,Pl	n	P
13- Diptera 1	B,Pa	n	OP
LEPIDOPTERA			
14- Lepidoptera 1	S	n	R
15- Lepidoptera 2	B	n	R
16- Lepidoptera 3	S	n	R
17- Lepidoptera 4	S,Pa,Pl	n	R
18- Lepidoptera 5	B	n	R
19- Lepidoptera 6	B	n	R

The mean number of visits per field trip varied across the flowering period in all MUs and was greater in the early months—especially in the slope MU (Fig. 2). The visitation means were more homogeneously distributed in the pasture MU.

Floral visitors were already active at 5:00 h and visited throughout the day. Although most visits occurred during periods of moderate temperatures, the timing of peak visitation differed among MUs (slope and pasture: 6:00 h–7:00 h; base of slope: 7:00 h–8:00 h; plantation: 8:00 h–9:00 h, Fig. 3). We observed no visits at the slope site during the evening (Fig. 3).

A total of nineteen invertebrate morphospecies was recorded during the study, (Table 2), including six bees (31.6%), six butterflies (31.6%), five wasps (26.3%) and two flies (10.5%). All floral visitors collected nectar; the bees *Apis mellifera*, *Centris* (*Trachina*) *fuscata*,

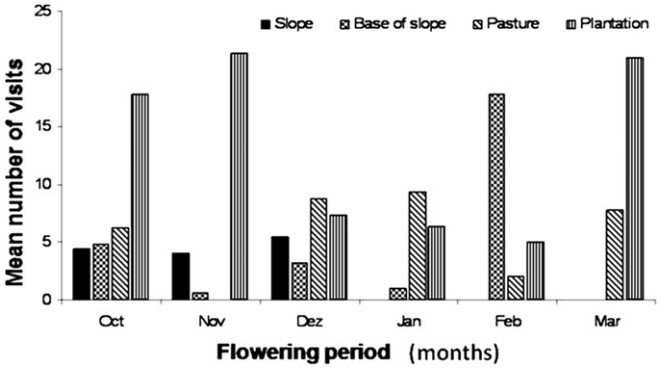

Fig. 2. Mean number of floral visits per field trip across the flowering period in populations of *Spondias tuberosa* Arruda (Anacardiaceae) subjected to different management regimes in an area of caatinga vegetation in Altinho, Pernambuco, Brazil.

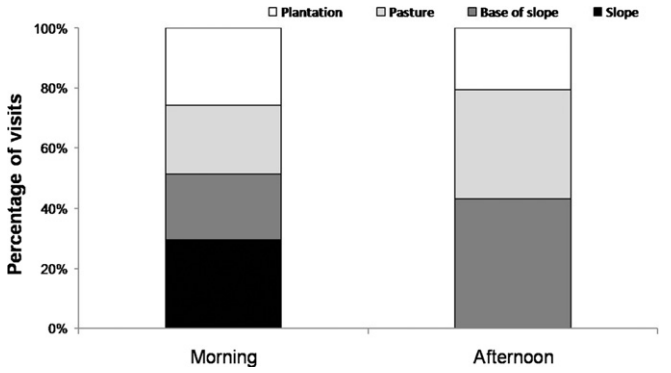

Fig. 3. Percentage of visits during the observation period in populations of *Spondias tuberosa* Arruda (Anacardiaceae) subjected to different management regimes in an area of caatinga vegetation in Altinho, Pernambuco, Brazil.

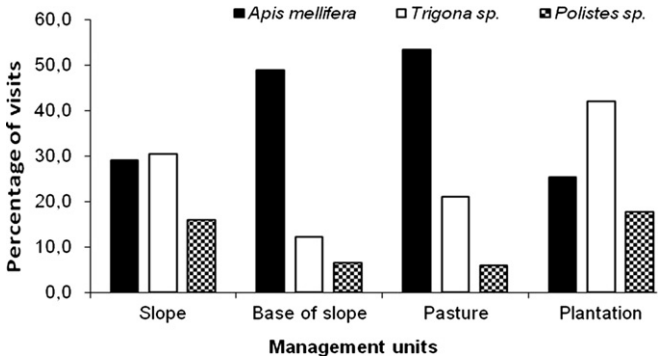

Fig. 5. Percentage of floral visits by the main pollinators in populations of *Spondias tuberosa* Arruda (Anacardiaceae) subjected to different management regimes in an area of caatinga vegetation in Altinho, Pernambuco, Brazil.

Frieseomelita sp. and *Trigona* sp. also collected pollen (Table 2). We observed ten morphospecies in the slope and plantation MUs and thirteen in the base-of-slope and pasture MUs; these values were not statistically different (x^2; = 0.78, $P = 0.85$).

In spite of the high number of species visiting *S. tuberosa* flowers, bees were responsible for more than 73.5% of visits, followed by wasps (18.9%), flies (4.1%) and butterflies (3.5%; Fig. 4). The distribution of visitation frequencies of distinct insect groups showed a similar pattern among all MUs (i.e., bee visits predominated) (Fig. 4). The bees *A. mellifera* and *Trigona* sp. and the wasp *Polistes canadensis* L, 1758 made the greatest contribution to the total number of visits and are considered the main pollinators of the species (Fig. 5).

Many species (13) were observed in more than one MU; in these cases, the MUs were contiguous (except for Lepidoptera unidentified *4*). Seven species (36%) were recorded in only one MU; the base-of-slope MU had the highest number of exclusive occurrences (21%).

A mellifera L., *Trigona* sp. and Apidae 1 were observed in all MUs. During its visits, *A. mellifera* caused the abscission of several flowers, a behavior that was not observed for other visitors. The relative contribution of *A. mellifera* to the total number of visits in each MU was greater in the pasture and base-of-slope MUs (53.3% and 48.9%, respectively) and lower in the slope and plantation MUs (29% and 25.3%, respectively; Fig. 6). The frequency of *Trigona* sp. was greater in the plantation and slope MUs (42% and 30.4%, respectively) and lower in the pasture and base-of-slope MUs (21% and 12.2%, respectively). Apidae 1 was considered to be an occasional pollinator because it was very small but eventually contacted sexual structures. In contrast, the bee *Plebeia* sp. did not contact sexual structures because of its small size and was considered to be a robber.

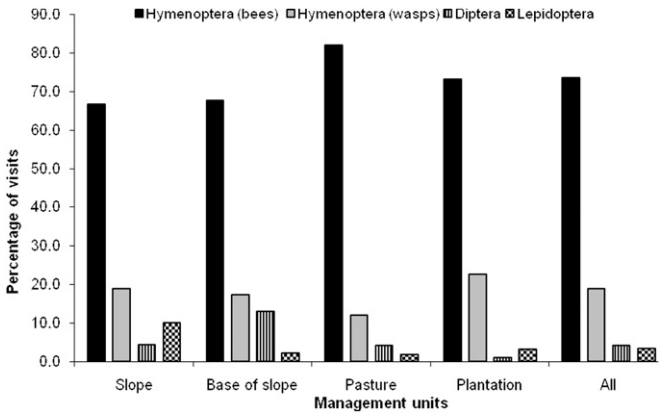

Fig. 4. Percentage of floral visits by different insect groups bees *A. mellifera* and *Trigona* sp. and the wasp *Polistes canadensis*, in populations of *Spondias tuberosa* Arruda (Anacardiaceae), subjected to different management regimes in an area of caatinga vegetation in Altinho, Pernambuco, Brazil.

Wasps were observed in all MUs but with greater frequency in the pasture and plantation MUs. Because of their large size and movement within the inflorescences, they acted as pollinators; it was sometimes possible to see pollen grains attached to their bodies, mainly on the mouthparts. Individuals of *Polistes canadensis*, one of the most common pollinators of *S. tuberosa* in the study area, were observed in the plantation and slope MUs (17.7% and 15.9%, respectively) and less frequently in the base-of-slope and pasture MUs (6.5% and 6%, respectively) (Fig. 5).

The two Diptera morphospecies were considered to be pollinators because they contacted sexual structures when walking on the inflorescence. Flies were observed more frequently in the pasture MU (12.9%) and less frequently in the plantation MU (1%); their visitation rate was similar in the slope and base-of-slope MUs (4.3 and 4.2%, respectively).

Lepidoptera species were the main group of robbers of *S. tuberosa* flowers. They visited more frequently at the slope site (10.1%) than in any other MU, with a low number of visits in the pasture MU (1.8%). These insects spent long periods of time in each flower (about 1 min) and visited only a few (less than four) flowers in each inflorescence.

The overall similarity among MUs in relation to floral visitor species was 48% (Jaccard coefficient = 0.489), but the pasture and plantation MUs presented similarity values of up to 80% (Fig. 6a). When robbers were excluded from the analysis, the similarity between the most disturbed areas diminished, and another group was formed joining the slope and base-of-slope MUs, showing 77% similarity (Fig. 6b). When data were analyzed from robbers alone, the pasture and plantation sites were identical (Jaccard coefficient = 1), forming a group with the slope MU with 33% similarity (Fig. 6c). These results show that the plantation and pasture MUs present the same patterns of differentiation as a function of floral visitors (pollinators or robbers).

4. Discussion and conclusion

This study is, to the best of our knowledge, the first to associate local management practices with the reproductive biology of species with economical and cultural importance in the semi-arid region of Brazil; many studies concerning this topic have been extensively developed in semi-arid ecosystems of Central America (Casas et al., 1999; Arias-Cóyotl et al., 2006; Oaxaca-Villa et al., 2006). In spite of the limitations due to the impossibility of replicating the management units that were studied, some important

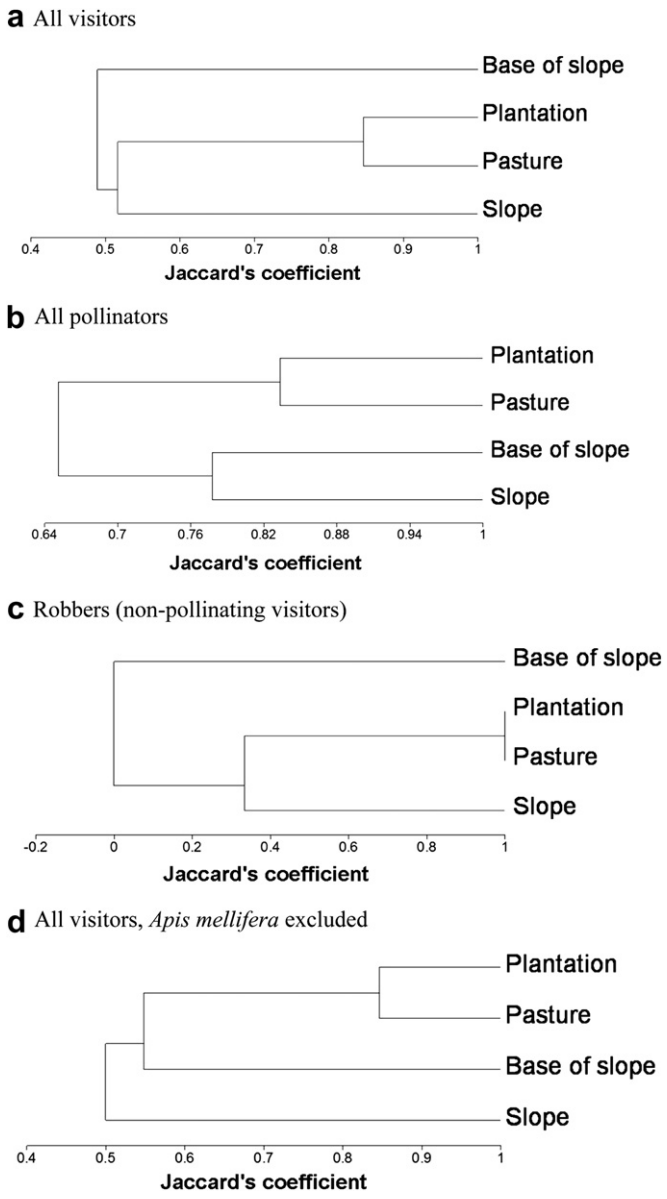

Fig. 6. Similarity among management units with respect to floral visitors in populations of *Spondias tuberosa* Arruda (Anacardiaceae) subjected to different management regimes in an area of caatinga vegetation in Altinho, Pernambuco, Brazil. a. All visitors; b. All pollinators; c. Robbers (non-pollinating visitors).

conclusions can be drawn regarding the influence of management practices on species with economic importance in the semi-arid region of Brazil.

The floral production recorded here is the same as that observed by Nadia et al. (2007) in a study of the floral biology of *S. tuberosa* in an area of caatinga with lower precipitation rates. However, our observations of flower production were lower than those recorded by another study that compared reproductive performance in *S. tuberosa* across different land uses in an area of caatinga and that reported a larger standard deviation (205.16 ± 180.31, Barreto, 2007). We observed greater flower production in the most managed areas, while Barreto (2007) found greater flower production in the most conserved areas. The apparent divergence between these results indicates that more studies are needed that use an appropriate experimental design. The problem is that the altered areas in which we developed our studies are a result of traditional practices of local communities, and they are distinct from the fragmentation scenario that is frequently found in many tropical forests. The greater flower production in the plantation MU may be interpreted as a response to abiotic conditions, such as higher levels of luminosity and temperature. Similar results have been found by several authors who have studied tree species in semi-arid regions (Murren, 2002; Fuchs et al., 2003; Quesada et al., 2004). This more conspicuous floral display may also be interpreted as a result of artificial selection by people, who prefer individuals with more flowers, as reported by Casas et al. (1999), in semi-arid vegetation. The greater flower production in the plantation MU may explain the higher visitation rate in this MU. Despite the high and variable flower production among MUs, fruit set was low and homogeneous among MUs. The low fruit set may be a consequence of the limiting conditions of the caatinga, which has an extremely dry season (Nadia et al., 2007), but it seems to be a common phenomenon of the Anacardiaceae family (Barreto, 2007). In contrast to what was recorded here, Barreto (2007) observed a greater fruit set of *S. tuberosa* in managed areas than in more conserved ones.

We may compare our findings with other studies, but we must be careful because plant species grow in different management scenarios. *Pachira chinata* (Jacq.) Alverson (Malvaceae), like *S. tuberosa*, is self-incompatible and produces more flowers in isolated individuals in open habitats than in individuals belonging to populations in continuous areas of dry forest; however, non-isolated individuals produce more fruits (Fuchs et al., 2003). These authors suggest that lower humidity levels may negatively influence the fruit set of isolated individuals (Fuchs et al., 2003). Other species, such as *Shorea siamensis* Miq. (Dipterocarpaceae) and *Anacardium excelsum* Skeels (Anacardiaceae), show low reproductive success under various extraction regimes in a humid ecosystem, mainly as a consequence of the isolation of individuals and consequently high levels of pollination between genetically close individuals (Ghazoul and McLeish, 2001). These data indicate a need for more studies concerning the impact of habitat alteration on the reproductive biology of plant species.

It is important to note, however, that the "natural experiment" nature of this study does not allow us to separate the effects of management from the inherent differences among the landscape positions, such as climatic ones, that could affect tree reproduction independently of local management. On the other hand, it is necessary to take into account that 1) the areas used in this study are very close one to another and 2) the local management practices may have produced or influenced different microclimates between the management units. Lins Neto et al. (2010) observed that mature fruits of *S. tuberosa* tend to present better "phenotypic features" (which are desirable for human consumption).

The high frequency of bees in all MUs is related to the melitophilous pollination syndrome of *S. tuberosa* (Barreto, 2007; Nadia et al., 2007). However, the floral and inflorescence morphology permits visits by a broad diversity of insect taxa. The greater visitation rates in the plantation MU, which were mainly by exotic or broadly distributed pollinators, indicate that isolation of individuals apparently does not represent a barrier to insect movement in the study area. Although these bees tend to maintain their nests in less managed areas in humid habitats (Samejima et al., 2004), they can also forage in more open areas of dry habitats (Oaxaca-Villa et al., 2006). Barreto (2007) confirms our findings because she observed a higher frequency of visits in managed areas than in conserved ones.

The high frequency of visits by the exotic bee *A. mellifera* and by species of *Trigona*, which is known to interfere with the relationships between plants and their native pollinators (Boiça Jr. et al., 2004), seems to be beneficial for *S. tuberosa*— especially in individuals of the plantation and pasture MUs. However, it is important to note that the behavior of *A. mellifera*, unlike that of native

visitors, can cause the premature abscission of flowers. Other studies have recorded pollination by *A. mellifera* in many fructiferous species in Brazil (Castro, 2006), including native caatinga species such as *Ziziphus joazeiro* Mart. (Rhamnaceae) (Nadia et al., 2007). An investigation of the influence of *A. mellifera* on native pollinators of the caatinga would be of great interest.

In the pasture and plantation MUs, there were individuals of *Prosopis juliflora* (SW.) DC. that are attractive to floral visitors, especially *A. mellifera* and *Trigona* sp. Other species that shared floral visitors with *S. tuberosa* included *Jatropha mollissima* (Pohl) Baill. (Euphorbiaceae), *Lantana camara* L. (Verbenaceae), *Cnidoscolus urens* (L.) Arthur (Euphorbiaceae), *Senegalia bahiensis* (Benth.) Seigler & Ebinger (Fabaceae-Mimosoideae), *Mimosa tenuiflora* Benth. (Fabaceae-Mimosoideae), *Chloroleucon extortum* Barneby & J.W. Grimes (Fabaceae-Mimosoideae), *Caesalpinia ferrea* Mart. (Fabaceae-Caesalpinioideae) and *Erythrina velutina* Willd. (Fabaceae-Faboideae). The low frequency of visits during the third month of flowering may also be explained by the onset of flowering of other species in the community that was preferred by *S. tuberosa* pollinators (pers. obs.), such as *M. urundeuva*, *P. juliflora* and *M. tenuiflora*, whose intensity of flowering was increased from January and October. The similar frequency of visits between areas with similar management conditions (i.e., plantation/pasture and slope/base of slope) may indicate that these areas present similar features that influence the access of floral visitors, such as abiotic conditions and resource availability at the community level.

Some general conclusions may be drawn from our case study. There are many indications that anthropogenic actions may affect *S. tuberosa* reproduction, but flower and fruit production appear to be weak predictors of differentiation among the MUs. On the other hand, the pollinator data improve our understanding of how the trees' reproductive biology is affected by habitat alteration in the study area. To obtain a greater comprehension of how and at what levels this process occurs, however, it is necessary to investigate, for example, gene flow among individuals of different MUs. This analysis could compare the reproductive phenology among these areas and compare nectar composition between *S. tuberosa* and other species that bloom simultaneously, testing the influence of resource features on visitation rates. Moreover, it is necessary to find other areas that can accommodate the requirements of more consistent experimental designs in which true replications are used. However, in spite of this limitation, our results allow us to affirm that, in the study area, the traditional management performed by local people does not affect the reproductive success of *S. tuberosa*, in contrast to what was recorded by other studies using slightly different approaches (Barreto, 2007) that observed much higher fruit production in managed areas.

Previous studies of reproductive biology in species subjected to anthropogenic action on semi-arid ecosystems (Oaxaca-Villa et al., 2006; Arias-Cóyotl et al., 2006); Casas et al., 1999; Lira and Casas, 1998) have focused on the impact of human action on the evolution and domestication of species with economic importance. Although we investigated a woody, endemic species, the applicability of ourstudy is broader because it indicates that the human action on species may affect the landscape dynamics. Modifications in the pollinator guild of one species indicate a new structure in plant–pollinator interaction within the community, and this indication has led us to consider landscape domestication. To the best of our knowledge, there are no similar studies in other arid or semi-arid environments.

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References

Aizen, M.A., Feinzinger, P., 1994a. Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. Ecology 75, 330–351.
Aizen, M.A., Feinzinger, P., 1994b. Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine "Chaco Serrano". Ecological Applications 4, 378–392.
Albuquerque, U.P., 1999. Manejo tradicional de plantas em regiões neotropicais. Acta Botanica Brasilica 13, 307–315.
Alencar, N.L., Araújo, T.A.S., Amorim, E.L.C., Albuquerque, U.P., 2009. Can the apparency hypothesis explain the selection of medicinal plants in an area of caatinga vegetation? A chemical perspective. Acta Botanica Brasílica 23, 910–911.
Alencar, N.L., Araújo, T.A.S., Amorim, E.L.C., Albuquerque, U.P., 2010. The Inclusion and selection of medicinal plants in traditional pharmacopoeias – evidence in support of the diversification hypothesis. Economic Botany 64, 68–79.
Araújo, E.L., Castro, C.C., Albuquerque, U.P., 2007. Dynamics of Brazilian caatinga – a review concerning plants, environment and people. Functional Ecosystems and Communities 1, 15–28.
Araújo, T.A.S., Alencar, N.S., Amorim, E.L.C., Albuquerque, U.P., 2008. A new approach to study medicinal plants with Tannins and Flavonoids contents from the local knowledge. Journal of Ethnopharmacology 120, 72–80.
Araújo, F.P., Oliveira, V.R., 2008. Produção de mudas de algumas espécies do gênero *Spondias*: uma alternativa na diversificação da fruticultura de sequeiro. In: Lederman, I.E., Lira Júnior, J.S., Silva Júnior, J.S. (Eds.), Spondias no Brasil: umbu, cajá e espécies afins. Empresa pernambucana de Pesquisa Agropecuária- IPA/UFRPE, Recife.
Arias-Cóyotl, E., Stoner, K.E., Casas, A., 2006. Effectiveness of bats as pollinators of *Estenocereus stellatus* (Cactaceae) in wild, managed in situ, and cultivated populations in La Mixteca Baja, central Mexico. American Journal of Botany 93, 1675–1683.
Ayres, M., Ayres- Jr., M., Ayres, D.L., Santos, A.A.S., 2003. BioEstat 3.0: Aplicações estatísticas nas áreas das ciências biológicas e médicas. Sociedade Civil de Mamirauá, Belém.
Barreto, L.S., 2007. Plano de manejo para conservação do umbuzeiro (*Spondias tuberosa*) e de seus polinizadores no Território Indígena Pankararé, Raso da Catarina, Bahia, Brasil. Dissertação, Universidade Estadual de Feira de Santana.
Boiça Júnior, A.L., Santos, T.M., Passilongo, J., 2004. Trigona spinipes (Fabr.) (Hymenoptera: Apidae) em Espécies de Maracujazeiro: Flutuação Populacional, Horário de Visitação e Danos às Flores. Neotropical Entomology 33, 135–139.
Casas, A., Valiente-Banuet, A., Rojas-Martínez, A., Dávila, P., 1999. Reproductive biology and the process of domestication of the columnar cactus *Stenocereus stellatus* in Central México. American Journal of Botany 86, 534–542.
Castro, M.S., 2006. Bee fauna of some tropical and exotic fruits: potential pollinators and their conservation. In: Kevan, P.G., Imperatriz-Fonseca, V.L. (Eds.), Pollinating Bees: The Conservation Link between Agriculture and Nature. Ministério do Meio Ambiente, Brasília, pp. 275–288.
Cavalcanti, N.B., Resende, G.M., Brito, L.T.L., 2000a. Processamento do fruto do imbuzeiro (*Spondias tuberosa* Arr. Cam.). Ciência e Agrotecnologia 24, 252–259.
Cavalcanti, N.B., Lima, J.B., Resende, G.M., Brito, L.T.L., 2000b. Ciclo reprodutivo do umbuzeiro (*Spondias tuberosa* Arr. Cam.) no semi-árido do Nordeste Brasileiro. Revista Ceres 47, 421–439.
Cavalcanti, N.B., Resende, G.M., Brito, L.T.L., 2001. Emergência e crescimento de plântulas de umbuzeiro (*Spondias tuberosa* Arruda) em diferentes substratos. EMBRAPA-CPATSA (Boletim de pesquisa), Petrolina.
CONDEPE/FIDEM., 2007. Perfil Municipal, Municípios da Região Agreste Central. http://www.municipios.pe.gov.br (cited 10.09.07).
Couvet, D., 2001. Deleterious effects of restricted gene flow in fragmented populations. Conservation Biology 16, 369–376.
Cunningham, S.A., 2001. Effects of habitat fragmentation on the reproductive ecology of four plant species in Mallee woodland. Conservation Biology 14, 758–768.
Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16, 265–280.
Fuchs, E.J., Lobo, J.A., Quesada, M., 2003. Effects of forest fragmentation and phenology on the reproductive success and mating patterns of the tropical dry forest tree *Pachira quinata*. Conservation Biology 17, 149–157.
Ghazoul, J., McLeish, M., 2001. Reproductive ecology of tropical forest trees in logged and fragmented habitats in Thailand and Costa Rica. Plant Ecology 153, 335–345.
Giulietti, A.M., Harley, R.M., Queiroz, L.P., Barbosa, M.R.V., Bocage Neta, A.L., Figueiredo, M.A., 2002. Espécies endêmicas da Caatinga. In: Sampaio, E.V.S.B., Giuietti, A.M., Vírginio, J., Gamarra-Rojas, C.F.L. (Eds.), Vegetação e Flora da Caatinga. APNE/CNIP. Associação de Plantas do Nordeste, Recife, pp. 103–118.

Leal, I.R., Tabarelli, M., Silva, J.M.C., 2003. Ecologia e conservação da caatinga: uma introdução ao desafio. In: Leal, I.R., Tabarelli, M., Silva, J.M.C. (Eds.), Ecologia e conservação da caatinga. Universitária – UFPE, Recife, pp. 5–12.

Leite, A.V.L., 2006. Sistema reprodutivo de plantas da caatinga: evidências de um padrão. Thesis, Universidade Federal de Pernambuco.

Lins Neto, E.M.F., Peroni, N., Albuquerque, U.P., 2010. Traditional knowledge and management of Umbu (*Spondias tuberosa*, Anacardiaceae): an endemic species from the Semi–Arid region of northeastern Brazil. Economic Botany 64, 11–21.

Lira, R., Casas, A., 1998. Uso y manejo de *Ibervillea millspaughii* (Cogn.) C. Jeffrey, Melothria pendula L. y otras especies silvestres de la familia Curcubitaceae: posibles procesos de domesticación incipiente. Boletin de la Sociedad Botánica de México 62, 77–89.

Lopes, A.V., Girão, L.C., Santos, B.A., Peres, C.A., Tabarelli, M., 2009. Long-term erosion of tree reproductive trait diversity in edge-dominated Atlantic forest fragments. Biological Conservation 142, 1154–1165.

Machado, I.C., Lopes, A.V., 2004. Floral traits and pollination systems in the caatinga, a Brazilian tropical dry forest. Annals of Botany 94, 365–376.

Moonen, A.C., Barberi, P., 2008. Functional biodiversity: an agroecosystem approach. Agriculture Ecosystems and Environment 127, 7–21.

Murren, C., 2002. Effects of habitat fragmentation on pollination: pollinators, pollinia viability and reproductive success. Journal of Ecology 90, 100–107.

Nadia, T.C.L., Machado, I.C., Lopes, A.V., 2007. Polinização de *Spondias tuberosa* Arruda (Anacardiaceae) e análise da partilha de polinizadores com *Ziziphus joazeiro* Mart. (Rhamnaceae), espécies frutíferas e endêmicas da caatinga. Revista Brasileira de Botânica 30, 89–100.

Oaxaca-Villa, B., Casas, A., Valiente-Banuet, A., 2006. Reproductive biology in wild and silvicultural managed populations of *Escontria chiotilla* (Cactaceae) in the Tehuacán Valley, Central Mexico. Genetic Resources and Crop Evolution 53, 277–287.

Pesci, R., 2004. Um novo humanismo e planejamento ambiental. In: Menegat, R., Almeida, G. (Eds.), Desenvolvimento sustentável e gestão ambiental nas cidades: estratégias a partir de Porto Alegre. Editora da UFRGS, Porto Alegre.

Quesada, M., Stoner, K.E., Lobo, J.A., Herrerias-Diego, Y., Palacios-Guevara, C., Munguia-Rosas, M.A., Salazar, K.A.O., Rosas-Guerrero, V., 2004. Effects of Forest fragmentation on pollinator activity and consequences for plant reproductive success and mating patterns in bat-pollinated bombacaceous trees. Biotropica 36, 131–138.

Salick, J., 1995. Toward an integration of evolutionary ecology and economic botany: personal perspectives on plant/people interactions. Annals of Missouri Botanical Garden 82, 25–33.

Samejima, H., Marzuki, M., Nagamitsu, T., Nakasizuka, T., 2004. The effects of human disturbance on a stingless bee community in a tropical rainforest. Biological Conservation 120, 577–587.

Sampaio, E.V.S.B., 2002. Uso das plantas da caatinga. In: Sampaio, E.V.S.B., Giulietti, A.M., Virgínio, J., Gamarra-Rojas, C. (Eds.), Vegetação e flora da caatinga. Associação Plantas do Nordeste – APNE. Centro Nordestino de Informações sobre Plantas – CNIP, Recife, pp. 49–90.

Santos, C.A.F., 1997. Dispersão da variabilidade fenotípica do umbuzeiro no semiárido brasileiro. Pesquisa Agropecuária Brasileira 32, 923–930.

Santos, L.L., Ramos, M.A., Silva, S.I., Sales, M.F., Albuquerque, U.P., 2009. Caatinga Ethnobotany: anthropogenic landscape modification and Useful species in Brazil's semi-arid northeast. Economic Botany. doi:10.1007/s12231-009-9094-3.

Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5, 8–32.

Silva, J.M.C., Tabarelli, M., 2000. Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. Nature 404, 72–73.

Tabarelli, M., Silva, J.M.C., Gascon, C., 2004. Forest fragmentation, synergisms and the impoverishment of neotropical forests. Biodiversity Conservation 13, 1419–1425.

Valentin, J.L., 2000. Ecologia numérica: uma introdução à análise multivariada de dados ecológicos. Interciência, Rio de Janeiro.

Wiens, D., Calvin, C.L., Wilson, C.A., Davern, C.I., Frank, D., Seavey, S.R., 1987. Reproductive success, spontaneous embryo abortion, and genetic load in flowering plants. Oecologia 71, 501–509.

Wyman, M., Gomez Villegas, Z., Miranda Ojeda, I., 2007. Land-use/land-cover change in Yucatán State, Mexico: an examination of political, socioeconomic, and biophysical drivers in Peto and Tzucacab. Ethnobotany Research Applications 5, 59–66.

Zar, J.H., 1996. Biostatistical Analysis. Prentice-Hall, New Jersey.